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Spatio-Temporal Patterns of Foraging Success for Fishes in an Illinois Stream

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16. ABSTRACT

Stomach contents of 10 fish species were examined to evaluate several scales of spatio-temporal variation in foraging success within an Illinois stream. Most species fed primarily on aquatic or terrestrial invertebrates, but one species specialized on fine detritus. Fish are a wide variety of invertebrate taxa, & diet overlap based on prey taxa was extensive among fish species & age classes. Foraging success, measured by number & size of prey eaten, varied among seasons, years, substrate composition & amounts of woody debris. However, no factor influenced foraging success of all species, & no 2 species responded identically to all factors. Fish generally fed most successfully in June, & least successfully in Oct. Some fish ate more or larger prey in a study area with gravel-cobble substrates than in a silt-sand area, & many ate more or larger prey in sites with woody debris than in sites from which debris was removed. In addition, aquatic invertebrates increased in abundance in silt-sand substrates when fish were excluded, but did not increase in gravel-cobble substrates, suggesting a greater potential for resource depression in the silt-sand area. Stream fishes apparently face continuous variation in food availability at several temporal & spatial scales. Because changes in availability are often unpredictable and influence each species differently, the competitive environment of stream fishes may be in a state of constant flux. Anthropogenic modifications of streams may create conditions that favor fishes such as certain cyprinids which have highly opportunistic feeding habits.

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Spatio-temporal Patterns of Foraging Success for Fishes in an Illinois Stream

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ABSTRACT: Stomach contents of 10 fish species were examined to evaluate several scales of spatio-temporal variation in foraging success within an Illinois stream. Most species fed primarily on aquatic or terrestrial invertebrates, but one species (*Pimephales notatus*) specialized on fine detritus. Fish ate a wide variety of invertebrate taxa, and diet overlap based on prey taxa was extensive among fish species and age classes. Foraging success, measured by number and size of prey eaten, varied among seasons, years, substrate composition and amounts of woody debris. However, no factor influenced foraging success of all species, and no two species responded identically to all factors. Fish generally fed most successfully in June, and least successfully in October. Some fish ate more or larger prey in a study area with gravel-cobble substrates than in a silt-sand area, and many ate more or larger prey in sites with woody debris than in sites from which debris was removed. In addition, aquatic invertebrates increased in abundance in silt-sand substrates when fish were excluded, but did not increase in gravel-cobble substrates, suggesting a greater potential for resource depression in the silt-sand area. Stream fishes apparently face continuous variation in food availability at several temporal and spatial scales. Because changes in availability are often unpredictable and influence each species differently, the competitive environment of stream fishes may be in a state of constant flux. Anthropogenic modifications of streams may create conditions that favor fishes such as certain cyprinids which have highly opportunistic feeding habits.

INTRODUCTION

Successful foraging is essential to reproduction of most animals; thus natural selection should favor individuals which are most efficient at obtaining food. Efficiency in foraging probably evolves in response to temporal and spatial variation in foraging success, which can result from inherent fluctuations in resource availability or from resource depression (*sensu* Charnov *et al.*, 1976) due to coexploiters. Resource depression may, in turn, generate strong competitive interactions and lead to the evolution of food partitioning. Among vertebrates, selective advantages of rapid growth and efficient foraging are perhaps best known for fishes. For example, rapid growth of fish to a relatively large size may be adaptive through increased gamete production (Bagenal, 1978) or immunity from predation (Werner *et al.*, 1983a) or success in dominance disputes. Thus, spatio-temporal patterns of fish foraging success may reveal information that is useful in understanding their population dynamics.

Aquatic or terrestrial invertebrates are the primary food resource of most fishes in small streams of the midwestern United States, whereas detritus, algae and other fish are less commonly consumed (Pflieger, 1975; Smith, 1979; Trautman, 1981). Although diets of most fish species are dominated by only one or two of these food resources, opportunistic feeding is widespread, and seasonal shifts in diet composition are common (Starrett, 1950; Whitaker, 1977). Furthermore, foraging rates often exhibit strong seasonal patterns (Mathur, 1977; Allan, 1981; Angermeier, 1982), which are probably induced by cycles of insect emergence and recruitment (Hynes, 1961; Resh, 1977). In addition to temporal variation, fish foraging patterns should also reflect spatial dynamics of invertebrate availability. For example, production and abundance of stream inverte-

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brates are typically lower in unstable substrates such as silt and sand than in stable substrates such as gravel and cobble (Wene and Wickliff, 1940; Resh, 1977; Waters, 1982) or woody debris (Benke *et al.*, 1984). However, relationships among habitat features (*e.g.*, substrate type) and foraging success of stream fishes remain largely unexamined.

Jordan Creek, a small stream in Illinois, is well-suited to examining effects of habitat features on foraging success of stream fishes for three reasons. First, upstream and downstream reaches of Jordan Creek differ markedly in current and substrate characteristics (Schlosser and Karr, 1981). Second, several cyprinid and centrarchid species are abundant in both reaches (Schlosser, 1982). Finally, most of the abundant species are widely distributed in the Midwest (Pflieger, 1975), and therefore may illustrate typical patterns for midwestern stream fishes. Based on this rationale, three hypotheses regarding spatio-temporal dynamics of fish foraging success were tested with comparative and experimental approaches:

H_1: Foraging success of fish in both reaches of Jordan Creek has a strong seasonal pattern.

H_2: Foraging success of fish in habitats with silt and sand substrates is lower than in habitats with gravel and cobble.

H_3: Foraging success of fish is higher in the presence of woody debris than in its absence.

Net caloric intake per unit time is perhaps the best measure of foraging success, but caloric content (per unit weight) of many aquatic and terrestrial invertebrates is similar (Cummins and Wuycheck, 1970). Therefore, knowledge of the number and size of consumed prey provides an alternative (albeit less precise) method for comparing foraging success of insectivorous fishes. In this study, foraging success was assumed to increase with the number or size of prey eaten. Furthermore, spatio-temporal patterns of these indices of foraging success were interpreted with respect to potential impacts of fish growth, survival and reproduction.

STUDY STREAM

Jordan Creek, a second-order tributary of the Salt Fork of the Vermilion River, is 17 km long, and drains a glaciated basin of 30 km^2 in E-central Illinois (Vermilion County). Riparian and channel characteristics change dramatically from recently channelized headwaters to relatively undisturbed downstream areas. Two of the four areas identified by Schlosser and Karr (1981) along this gradient were selected as sample areas for this study. The upstream area, last channelized in the 1940s, features a narrow (5-10 m) strip of riparian vegetation dominated by multiflora rose (*Rosa multiflora*) and hackberry (*Celtis occidentalis*). Because the stream in this area has only a slight gradient (0.7 m/km), pool-riffle structure is poorly developed, and bottom substrates are 85% silt and sand (Angermeier, 1983). In contrast, the downstream area, which has never been channelized, is typically bordered by a broad (10-50 m) strip of woodland comprising mostly maples (*Acer* spp.), oaks (*Quercus* spp.), sycamore (*Plantanus occidentalis*) and ash (*Fraxinus* spp.). Steeper gradient (4.0 m/km) in this area is associated with well-developed pool-riffle structure and substrates composed of 52% gravel and cobble (Angermeier, 1983). Surface discharge in both areas is supplemented by subsurface springs, and rarely drops to zero. Water temperature did not differ substantially between the two study areas. Temperature ranges were 20-23C in June, 21-23C in August, and 6-14C in October. Although the two study areas differed in a variety of habitat parameters, substrate differences were judged to be most important with regard to production of fish food resources. Thus, the two areas will be hereafter distinguished as the "silt-sand" area and the "gravel-cobble" area.

MATERIALS AND METHODS

Fish sampling design. — Fish were collected from 35-m reaches located in pools or raceways. Collections were drawn from 13 reaches of the silt-sand study area in each of four

collection periods from June 1980 through April 1981 (June, August, October and April). The number of sample reaches was increased for collections in June, August and October 1981: 15 reaches from the silt-sand area were sampled during each of these periods, and 10 reaches from the gravel-cobble area were sampled. This design permitted comparisons of dietary patterns between 1980 and 1981 (in the silt-sand area only) and between the two study areas (1981 only).

Effects of woody debris on dietary habits were assessed by manipulating the amount of woody debris in certain sample reaches. All reaches received one of three experimental treatments: control, artificial-debris or no-debris. Debris in control reaches was not manipulated; there were three reaches in 1980 and April 1981, but 10 in the remainder of 1981 (six in the silt-sand area, and four in the gravel-cobble area). All woody debris was removed from other sample reaches in May 1980 and 1981, and naturally occurring debris was removed thereafter as it entered those reaches. Some of the reaches from which debris was removed remained as no-debris reaches; there were six no-debris reaches in 1980 and April 1981, and three in each study area from June through October 1981. Artificial-debris structures, constructed from pine boards, were installed in the rest of the reaches from which natural woody debris was removed. Each structure provided approximately 1.0 m^2 of surface area which was rapidly colonized by aquatic invertebrates (Angermeier and Karr, 1984). Each artificial-debris reach received 8-16 structures, thereby increasing woody debris abundance to levels greater than those observed in control reaches.

Fish exclosures.—Small rectangular exclosures (65 x 80 cm) were erected to compare the relative potential for resource depression (Charnov *et al.*, 1976) between the two study areas. Exclosures were constructed of hardware cloth (0.32-cm mesh) supported by steel posts. The cloth extended 10 cm into the stream bottom and 65-80 cm above the bottom. Exclosures were set up in pairs consisting of an "open" and a "closed" unit, which were beside each other and 15 cm apart. Paired units were identical except that the open exclosure lacked a downstream panel, thereby allowing free access to fish. A guard screen (2.5 x 1.3 cm mesh) was installed 5 m upstream from each pair of exclosures to prevent organic debris from fouling the hardware cloth. Experiments were conducted from 7-28 June and from 7-28 September 1981; three pairs of exclosures were maintained in each study area during each experiment. Exclosures were removed from the stream between experiments.

Exclosure sites were located in raceway or shallow pool habitats, and were selected to provide similar depth, current and substrate characteristics for both units. Water depth inside exclosures ranged from 25-55 cm; current velocity outside exclosures ranged from 0-0.5 m/s, but was reduced inside exclosures.

At the end of each experiment, benthic invertebrates were collected from each exclosure, using a Surber sampler (0.093 m^2; 240 μm mesh). Although Surber samples are known to be quite variable (*e.g.*, Needham and Usinger, 1956), one sample from each exclosure was judged to be adequate because of the relatively large portion of the total bottom area included in each sample (18%) and the extreme homogeneity of the stream bottom inside each exclosure. Invertebrate samples were preserved immediately in 15% formalin, then later split into eight subsamples with a device similar to that of Waters (1969). Previous work indicated that subsamples generated from this device were consistently similar (Schlosser, 1982; Angermeier, 1983). All invertebrates from a randomly chosen subsample of each Surber sample were identified and measured (body length to the nearest 0.1 mm) beneath a microscope.

Fish collection.—Fish were collected separately from each sample reach during each sampling period. Collections were performed in 3-6 reaches per day between 0900 and 1600 hr, and all were completed within a 10-day period. Fish sampling proceeded by blocking both ends of a sample reach with nets (0.5-cm mesh), then electric-seining the reach twice. The electric seine was 7 m long, and powered by a gasoline generator with 20 amp (120 volts, AC) maximum capacity (Angermeier, 1983; Larimore, 1961).

Stunned fish were collected in dip-nets or block-nets. Fish to be used in gut analyses were randomly selected from those collected, killed immediately in a tricaine methanesulfonate solution, and preserved in 30% formalin. The number of fish preserved from each species and size class was roughly proportional to the number collected. The 10 most abundant species in the collections were used for the following analysis.

Dietary analysis.—The stomach (for centrarchids) or anterior third of the gut (for other fish taxa) of each preserved specimen was dissected under a microscope. Prey were identified to family when possible; an ocular micrometer was used to measure body length to the nearest 0.1 mm. All prey of terrestrial origin were treated as a single taxon. Prey fragments that could not be confidently identified (*i.e.*, counted and estimated to length as individual prey) were excluded from the analysis. Presence of non-animal foods (*e.g.*, seeds, detritus) was noted, but abundance was not quantified.

Fish were grouped into species and size classes for analysis of feeding habits. Plots of length-frequency distributions were used to assign specimens of five species into size classes corresponding to age-0 (young of year) and age-1 (surviving one winter) groups. Age-0 and age-1 blackstripe topminnow (*Fundulus notatus*), bluntnose minnow (*Pimephales notatus*) and spotfin shiner (*Notropis spilopterus*) were not clearly distinguishable on the basis of length, and were pooled for analysis. Specimens of smallmouth bass (*Micropterus dolomieui*) and bluegill (*Lepomis macrochirus*) were restricted to age-0 and age-1 groups, respectively. Specimens older than age-1 were uncommon for all species, and were excluded from the analysis. Most species examined were common in both study areas, but blackstripe topminnow and spotfin shiner were too rare in the gravel-cobble and silt-sand areas, respectively, to warrant dietary analysis.

Fish consume prey of a wide variety of sizes, and size distributions are frequently skewed. Moreover, large prey are energetically more profitable to a predator than small prey (Werner *et al.*, 1983b), and should be weighted more heavily in considerations of foraging success. Thus, simple central-tendency descriptors of prey size distribution (*e.g.*, mean, median) were judged to convey too little information to adequately relate prey size to foraging success. As an alternative, prey were grouped into three arbitrary length classes: small (<3.00 mm), medium (≥ 3.0 mm and ≤ 9.0 mm) and large (>9.0 mm). Prey-size distributions of fish from different years and habitats were then compared by means of the G-test for independence with Williams' correction (Sokal and Rohlf, 1981). This test was also used to compare frequencies of occurrence of food types in fish from different years and habitats.

Season, year, study area and abundance of woody debris were all expected to influence dietary patterns of fish. However, because they all covaried in the sample design, individual effects of these variables could not be cleanly partitioned. Therefore, a multiple regression model was used to estimate the effects of year, study area and woody debris, while statistically holding other variables constant. Regression analyses were performed on log-transformed values of the prey number per fish [*i.e.*, $\log_{10}$ (prey number + 0.01)]; number of aquatic and terrestrial prey were treated separately. The four variables were treated as follows: "season" was represented by three dummy variables; "year" and "study area" took one of two values (1 or 2); "wood debris" was assigned a 1, 3 or 5, which corresponded to no-debris, control and artificial-debris treatments, respectively.

RESULTS

GENERAL DIETARY PATTERNS

Stomach contents of fish were grouped into five major categories: aquatic invertebrates, terrestrial invertebrates, other fish, plant material, and detritus. Aquatic invertebrates, an important dietary component for all species examined, occurred in fish stomachs more frequently than any other food type, and were especially prevalent in diets of the four centrarchid species (Table 1). Terrestrial invertebrates were second in frequency of occurrence, and were especially common in stomachs of spotfin shiner and creek

TABLE 1.—Frequencies of occurrence of five major food resources in 10 fish species of Jordan Creek, Illinois. Data from all collections were pooled

Species	Fish			Percent of individuals containing:				
	Total length (mm)	Age	Number examined	Aquatic invertebrates	Terrestrial invertebrates	Other fish	Plant material	Detritus
blackstripe topminnow	37-74	0-1	121	53	22	0	0	0
bluntnose minnow	35-89	0-1	520	11	<1	0	3	69
creek chub	25-74	0	77	43	36	1	10	5
creek chub	75-124	1	45	33	33	2	16	2
hornyhead chub	30-64	0	554	57	5	0	4	3
hornyhead chub	65-149	1	449	43	9	0	9	3
spotfin shiner	30-89	0-1	133	35	44	2	9	0
striped shiner	30-59	0	372	35	25	<1	8	1
striped shiner	60-139	1	435	27	31	0	18	6
smallmouth bass	45-114	0	54	80	13	20	2	0
rock bass	25-59	0	65	88	3	0	0	0
rock bass	60-104	1	27	78	22	0	0	0
bluegill	50-99	1	59	95	22	0	2	0
longear sunfish	25-59	0	131	94	2	0	0	0
longear sunfish	60-99	1	156	81	22	0	0	0

chub (*Semotilus atromaculatus*). Smallmouth bass was the only species that regularly consumed other fish. Plant material (filamentous algae, fruits, seeds, etc.) was occasionally eaten by most fish species, but occurred most frequently in stomachs of creek chub and striped shiner (*Notropis chrysocephalus*) and was more common in age-1 fish than in age-0 fish. Bluntnose minnow was the only species that specialized on detritus (an amorphous aggregate of fine organic and inorganic particles). The proportion of stomachs that were totally empty was generally $<10\%$, and ranged from 2% for bluegill to 23% for age-1 hornyhead chub (*Nocomis biguttatus*).

A cluster analysis of unweighted pair-groups (Sneath and Sokal, 1973) was performed on the food-type occurrence data. This analysis indicated that the 15 fish groups comprised four trophic guilds (Fig. 1): aquatic insectivores, generalized insectivores, insectivore-piscivores and detritivores. Smallmouth bass was the only insectivore-piscivore, and bluntnose minnow was the only detritivore. Generalized insectivores included all age-classes of creek chub, spotfin shiner and striped shiner; aquatic insectivores comprised the remaining five species. Feeding habits of conspecific age-classes were typically no more similar than habits of equal-age fish of different species.

Because aquatic or terrestrial invertebrates were important components of all fishes' diets, consumption patterns for these two resources were examined in more detail. All identified prey items (including fish) were grouped into one of 18 taxonomic categories (Appendix A). Dipteran larvae (mostly chironomids) were by far the most commonly eaten prey, and were especially abundant in stomachs of longear sunfish (*Lepomis megalotis*). The Shannon-Wiener index (H') was used as an index of diet breadth for the animal portion of each fish group's diet (Table 2). H' ranged from 1.02 for bluntnose minnow to 2.09 for age-1 rock bass (*Ambloplites rupestris*). Average diet breadths for generalized and aquatic insectivores were similar ($\bar{x}$s = 1.59 and 1.76, respectively). Although some prey taxa (*e.g.*, crayfish, cladocerans) were eaten by only one fish species, most occurred in stomachs of several species.

PATTERNS OF FORAGING SUCCESS

Effects of season.—Most fish groups exhibited significant seasonal patterns in the number of prey found in their stomachs (Fig. 2); exceptions were bluegill, age-1 creek chub and age-0 hornyhead chub. Bluntnose minnow and age-0 striped shiner were the only groups that contained the most prey in April. More commonly, fish contained the most prey in June and relatively few prey in October. Terrestrial prey seldom outnumbered aquatic prey, and were most common in June and August samples. The relative abundance of terrestrial prey in stomachs of generalized insectivores was highest in August. Late summer declines in number of prey eaten by some generalized insectivores coincided with increases in the occurrence of detritus. For example, age-1 striped shiners collected in August or October contained detritus more frequently than those collected in April or June (7.2 vs. 2.3%; G-test, $p<0.05$). Similar, but nonsignificant trends were also observed for age-0 striped shiner and age-0 creek chub. In contrast, aquatic insectivores did not increase their consumption of other food types during seasons of low invertebrate consumption. Overall, these consumption patterns suggest that invertebrate availability for many fish declines substantially from early summer (June) through autumn (October), and strategies for coping with changes in the food base vary among species.

Effects of year.—One-third of the fish groups contained significantly more prey in 1980 than in 1981 (Table 3). Age-0 and age-1 creek chub, age-1 hornyhead chub and age-0 longear sunfish contained more aquatic prey in 1980 than in 1981; age-0 creek chub and age-0 and age-1 striped shiner contained more terrestrial prey in 1980 than in 1981. In contrast, only bluntnose minnow contained more prey in 1981 than in 1980. Age-1 striped shiner consumed more aquatic prey in 1980 than in 1981, but exhibited the opposite pattern for terrestrial prey; thus, total prey consumption for age-1 striped shiner was similar in both years. Size distributions of the prey in these fish were gener-

ally similar for 1980 and 1981 (comparing prey from the silt-sand reach only). The only exception was age-0 longear sunfish, which ate larger (but fewer) prey in 1981 than in 1980 (G-test; $P<0.001$). Other between-year differences in prey size distribution were observed for smallmouth bass (larger prey in 1981; $P<0.001$) and bluegill (larger prey in 1980; $P<0.001$). In addition to invertebrate prey, other foods were consumed by some fishes more frequently in 1980 than in 1981 (G-test; $P<0.05$). For example, bluntnose minnow, age-0 hornyhead chub and age-0 striped shiner ate detritus more often in 1980, and age-1 striped shiner ate detritus and plant material more often in 1980. Overall, feeding habits of most fish did not differ markedly in 1980 and 1981. However, those groups exhibiting significant between-year differences in foraging success (as indicated by prey number and a food's frequency of consumption) tended to eat more in 1980 than in 1981.

Effects of woody debris. — Occurrence of woody debris was positively correlated with the number of prey in stomachs of spotfin shiner and smallmouth bass, but negatively correlated with the number of prey in blackstripe topminnow and age-0 longear sunfish (Table 3). Blackstripe topminnow and age-0 longear sunfish also ate smaller prey in the presence of artificial debris than in its absence, but five other fish groups ate larger prey in the presence of artificial debris than in its absence (Fig. 3). For some fish, there was an interaction between the effects of woody debris and study area. Effects of woody debris on prey size were apparent for age-0 longear sunfish, bluntnose minnow and age-1 striped shiner in the silt-sand area ($P<0.05$), but were not observed in the gravel-cobble area. No fish groups exhibited effects of woody debris on prey size in the gravel-cobble area, but not in the silt-sand area. Prey size distributions of fish collected from control reaches in both areas were typically more similar to those from artificial-debris reaches than to those from no-debris reaches. Overall, nearly half of the fish groups consumed more prey or larger prey in the presence of woody debris than in its absence.

Effects of study area. — Invertebrate prey number, prey size, prey taxa and the use of other foods differed among fish collected from the two study areas. Although most fish groups exhibited some dietary differences between the silt-sand and gravel-cobble areas, no group differed in all diet parameters. Age-0 creek chub contained more terrestrial prey, and age-0 striped shiner and age-1 hornyhead chub contained more aquatic prey in the gravel-cobble study area than in the silt-sand area (Table 3). Age-1 striped shiner, which consumed similar proportions of terrestrial and aquatic prey, contained more

TABLE 2. — Diet breadths (H′) based on prey taxa for 15 fish groups from Jordan Creek. Blank cells occur for fish uncommon in one of the study areas

Fish species (Age)	H′		
	Combined data	Silt-sand	Gravel-cobble
bluntnose minnow (0-1)	1.02	0.86	0.86
creek chub (0)	1.63	1.89	1.11
creek chub (1)	1.85	1.85	—
striped shiner (0)	1.64	1.47	1.32
striped shiner (1)	1.48	1.51	1.06
spotfin shiner (0-1)	1.35	—	1.35
blackstripe topminnow (0-1)	1.59	1.59	—
hornyhead chub (0)	1.55	1.59	1.24
hornyhead chub (1)	1.94	1.92	1.19
smallmouth bass (0)	1.17	0.99	1.10
rock bass (0)	2.01	1.86	1.68
rock bass (1)	2.09	1.96	1.85
bluegill (1)	1.80	1.44	1.07
longear sunfish (0)	1.39	1.42	1.19
longear sunfish (1)	1.07	1.78	0.70

aquatic prey in the silt-sand area, but more terrestrial prey in the gravel-cobble area. However, prey size was larger for age-1 striped shiner in the gravel-cobble area than in the silt-sand area (Fig. 4). Bluntnose minnow, which contained similar numbers of prey in both study areas, also ate larger prey in the gravel-cobble area (Fig. 4). Bluegill and age-0 and age-1 longear sunfish contained similar prey numbers in both study areas, but ate larger prey in the silt-sand area (Fig. 4).

Some of the differences in prey size observed between the two study areas were readily attributable to taxonomic composition of prey. For example, 94% of the prey eaten by bluntnose minnow in the silt-sand study area were microcrustaceans (ostracods and cladocerans); these taxa made up less than 1% of bluntnose minnow prey in the gravel-cobble area, where they were replaced by larger dipteran (62%) and trichopteran (30%) larvae. Similarly, bluegill prey in the gravel-cobble reach were predominantly copepods (67%) and water mites (11%); these taxa made up less than 1% of bluegill prey in the silt-sand area, and were replaced by dipteran larvae (51%), amphipods (16%) and hemipterans (16%). All fish groups except smallmouth bass exhibited greater diet breadth (based on prey taxa) in the silt-sand study area than in the gravel-cobble area (Table 2). Age-1 rock bass consumed the broadest diet in both study areas, but in general the rank-order of diet breadths was not concordant between study areas (Kendall's tau; $P > 0.05$).

In addition to differences in invertebrate consumption between the two study areas, some differences in the use of other foods were also apparent. For example, plant material, a secondary food resource, was eaten more frequently by age-0 hornyhead chub and striped shiner and age-1 striped shiner in the gravel-cobble study area than in the silt-sand area (G-test; $P < 0.05$).

In summary, most fish consumed a wider variety of prey taxa in the silt-sand study area than in the gravel-cobble area, and five fish groups ate fewer or smaller prey in the

TABLE 3.—Significance of F-ratio probabilities from multiple regression analyses of numbers of prey found in stomachs of selected fish groups. Dashed entries indicate insufficient data to include that variable; blank entries indicate a nonsignificant ($p > 0.05$) F-ratio for that variable. "•" indicates $0.01 \leq p < 0.05$; "••" indicates $0.001 \leq p < 0.01$; "•••" indicates $p < 0.001$

Fish species (age)	Prey Type*	Significance of F-ratio		
		Year	Area	Debris
bluntnose minnow (0-1)	A	•••		
creek chub (0)	A	•		
	T	•	•••	
creek chub (1)	A	•	---	
striped shiner (0)	A		••	
	T	•••		
striped shiner (1)	A	•	•	
	T	•••	•••	
spotfin shiner (0-1)	A	---	---	•
	T	---	---	
blackstripe topminnow (0-1)	A	---	---	•
hornyhead chub (0)	A			
hornyhead chub (1)	A	••	•••	
smallmouth bass (0)	A			•
rock bass (0)	A			
rock bass (1)	A			
bluegill (1)	A			
longear sunfish (0)	A	••		•
longear sunfish (1)	A	---		

*A = Aquatic; T = Terrestrial

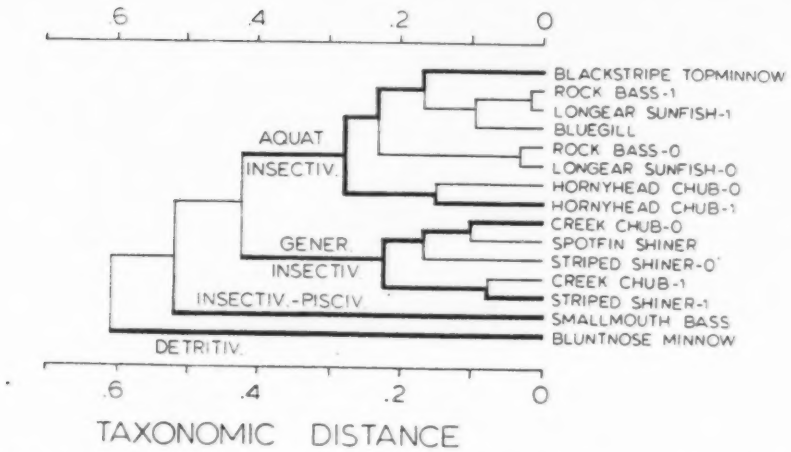

Fig. 1.—Dendogram of cluster analysis based on food-type frequency in Jordan Creek fishes (Table 1). The cluster analysis used unweighted pair groupings of average taxonomic distance based on five characters (food-types); cophenetic correlation coefficient = 0.88. Four trophic guilds are shown: aquatic insectivore, generalized insectivore, insectivore-piscivore and detritivore

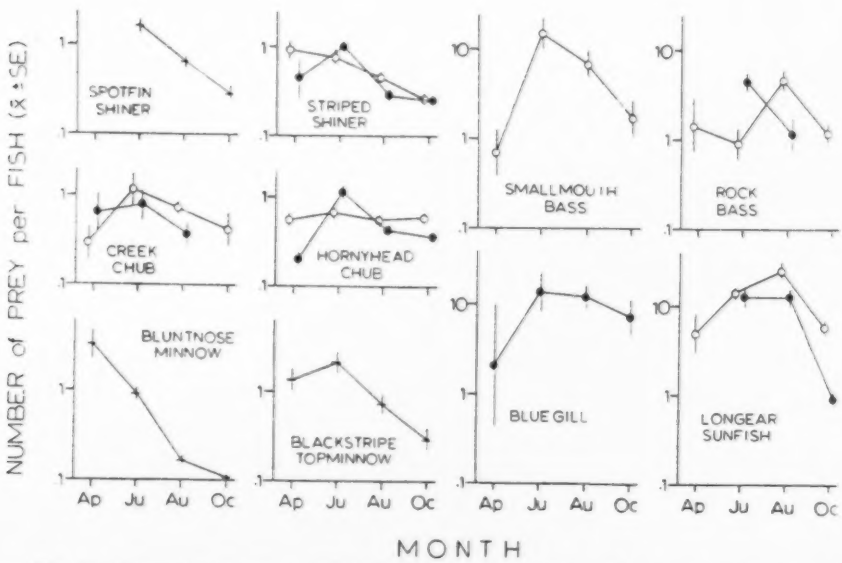

Fig. 2.—Seasonal changes in number of prey (log scale) identified from specimens of 10 fish species of Jordan Creek. Sample size for each plotted point ranged from 3-236; data from 1980 and 1981 were pooled. Open circles represent age-0 fish, closed circles represent age-1 fish; dashes were used for species in which age-0 and age-1 fish were not distinguished

silt-sand area. However, three aquatic insectivore groups ate larger prey in the silt-sand area. Fish from the two study areas commonly consumed different prey taxa. This tendency was often associated with differences in prey size, but was not closely associated with differences in prey number. Alternate foods (*e.g.*, plant material) were eaten more frequently in the gravel-cobble area.

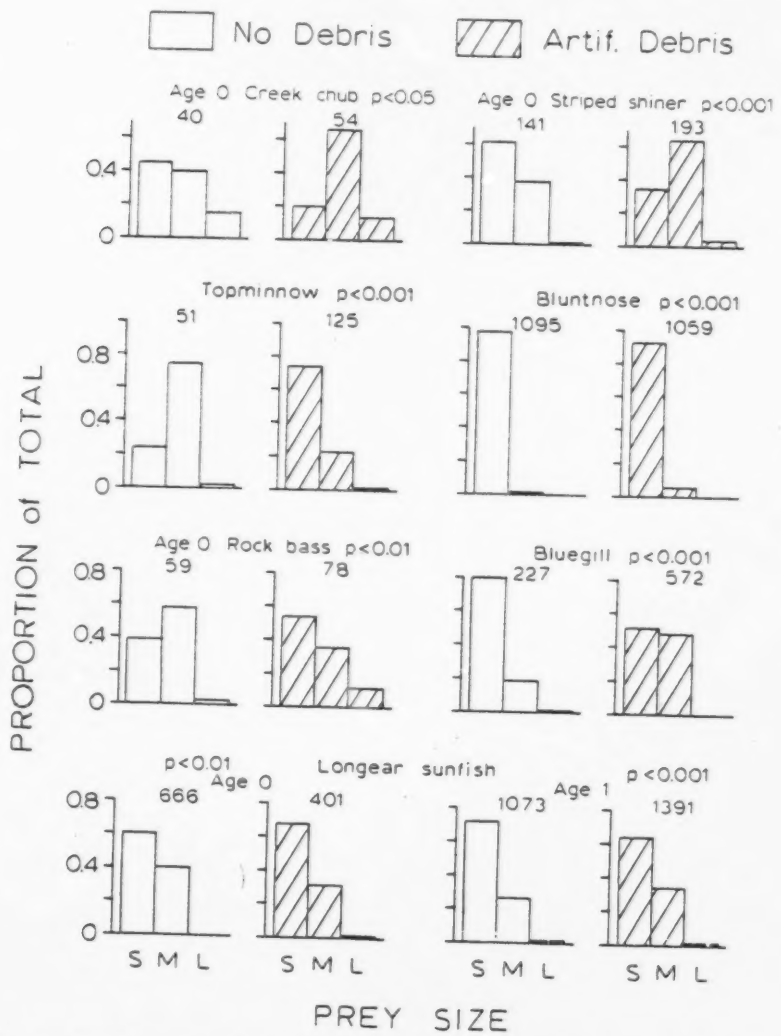

Fig. 3.—Size frequency distributions of prey eaten by selected fish groups in study reaches with and without artificial woody debris. Small prey were <3.0 mm long, large prey were >9.0 mm long. Numbers above distribution indicate sample sizes. Significance of G-test comparisons are also given

FISH EXCLOSURE EXPERIMENTS

Dietary patterns of some fish groups suggested that invertebrate prey might be generally less available in the silt-sand study area than in the gravel-cobble area. As an independent test of this hypothesis, fish exclosure experiments were conducted to compare accumulation rates of consumable prey in the two study areas in the absence of fish predators. If the silt-sand area featured a greater potential for resource depression (Charnov *et al.*, 1976), it was also expected to exhibit a more pronounced increase in prey abundance when fish were excluded.

Data from the June and September experiments were pooled because of the small number of replicates in each. Total invertebrate densities in all exclosures ranged from 917/m² to 17,500/m² in the silt-sand area, and from 1500/m² to 6667/m² in the gravel-cobble area. The most abundant invertebrate taxa were dipteran larvae, coleopteran larvae, and copepods, all of which were commonly eaten by fish (Appendix A). Pairwise comparisons of densities indicated that "open" exclosures in the silt-sand area supported fewer total invertebrates and fewer large invertebrates, as well as fewer dipteran larvae, coleopteran larvae and copepods, than "closed" exclosures (Wilcoxon signed-rank test; $P < 0.05$). In contrast, "open" exclosures in the gravel-cobble area did not support fewer invertebrates from any of these categories than "closed" exclosures, thereby suggesting that impacts of fish consumption on invertebrate abundance were less severe than in the silt-sand area. Observed differences between the study areas in effects of exclosures can-

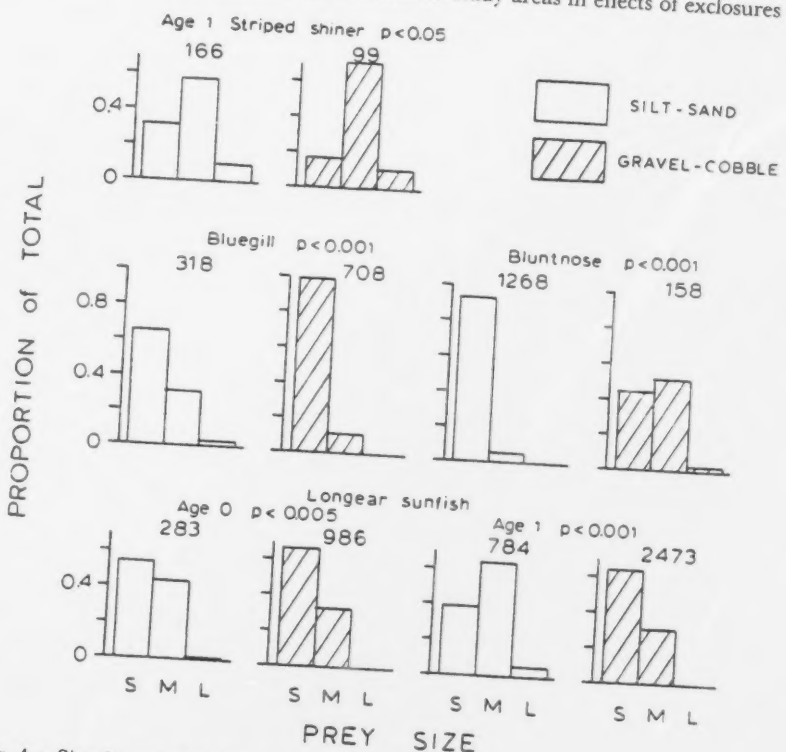

Fig. 4.—Size frequency distributions of prey eaten by selected fish groups in the silt-sand and gravel-cobble study areas. Format is the same as Figure 2

not be simply attributed to fluvial changes induced by the exclosures themselves, because all exclosures appeared to disrupt stream hydraulics to a similar degree. For example, fine silt particles were deposited inside all exclosures throughout the experiments. In conclusion, results of these experiments support the hypothesis that potential for resource depression among insectivorous fish was greater in the silt-sand study area than in the gravel-cobble area.

DISCUSSION

Patterns of food consumption by Jordan Creek fishes are probably typical of those in small streams of North America, where species feeding predominantly on aquatic and terrestrial invertebrates (*i.e.*, insectivores) are ubiquitous (Lee *et al.*, 1980). Although species that largely eat plant material, fish or detritus are less numerous, they are still important components of the fish community, especially where populations attain high densities. Insectivorous fishes commonly consume a wide variety of invertebrate taxa (Pasch and Lyford, 1972; Mendelson, 1975; Angermeier, 1982), and exhibit extensive diet overlaps if prey are defined on the basis of taxonomy. Similar patterns were observed in this study for both aquatic and generalized insectivores, but the least insectivorous species (bluntnose minnow) often consumed small taxa not eaten by other fishes. Although differences in taxonomic composition between fish diets may indicate ecological segregation, behavioral parameters of the predator (*e.g.*, foraging height in the water column) may be more accurate indices of niche relationships (*see* Mendelson, 1975).

All fish in this study exhibited temporal or spatial variation in foraging success, as measured by number or size of consumed prey. Seasonal variation in foraging rates are common among stream fishes (Mathur, 1977; Allan, 1981; Angermeier, 1982), and stem from annual reproductive cycles of aquatic insects (Hynes, 1961; Resh, 1977). Widespread insect emergence during summer often results in an early autumn scarcity of prey for insectivorous fish (Finger, 1982; Schlosser and Toth, 1984) because of reductions in abundance and size of insects (Angermeier, 1982; Angermeier and Carlson, 1985). In Jordan Creek this scarcity is exacerbated by relatively high water temperature and the pulsed recruitment of young-of-year fish, most of which also eat aquatic invertebrates. Foods other than aquatic insects also fluctuate in availability seasonally, but their patterns are less well-known. Peak consumption of terrestrial invertebrates by Jordan Creek fishes in June and August is consistent with other studies (Starrett, 1950; Allan, 1981), and with intuitive expectations regarding activity of terrestrial invertebrates. Detritus is probably most available after extended periods of low flow, such as those often occurring in late summer. Some generalized insectivores in this study (*e.g.*, striped shiner) compensated for low invertebrate availability in October by increasing their consumption of detritus, but the more specialized aquatic insectivores did not eat alternate foods. Similarly, Starrett (1950) reported greater consumption of "ooze" by cyprinids during low-flow periods.

Annual cycles of food availability may be modified by unpredictable between-year variation in flow regime. Rainfall near Jordan Creek from July through October 1980 was low (290 mm; 30-year $\bar{x} = 343$ mm), causing stream discharge to decline steadily through the summer (Angermeier, 1983). In contrast, rains were exceptionally heavy from July through October 1981 (544 mm), and caused recurrent periods of elevated discharge. Differences in flow regime were manifest in depth and current characteristics and were reflected in consumption patterns of several fish groups. Foraging success was enhanced for some species in 1980 by build-ups in populations of pool-dwelling invertebrates such as corixids, copepods and cladocerans. Some fish also ate more terrestrial invertebrates and detritus in 1980, apparently because of low, stable flow conditions. In larger streams, where fish can exploit food-rich floodplains, fish abundance (Ross and Baker, 1983) and productivity (Holcick and Bastl, 1977) may be correlated with flooding. But in Jordan Creek, where discharge volume rarely exceeds the banks, the usual

effect of increased flow is to scour accumulations of invertebrates, algae and detritus. Because annual variation in discharge is more pronounced in small streams than in larger ones (Horwitz, 1978), between-year differences in food availability are probably also greater in small streams.

In addition to temporal scales of variation in food availability, stream fishes also encounter spatial variation in stream characteristics that influence food availability. Although relationships between vegetation features and availability of terrestrial invertebrates for stream fishes are virtually unknown (*but see* Angermeier and Karr, 1983), greater consumption of terrestrial invertebrates by creek chub and striped shiner in the gravel-cobble area than in the silt-sand area of Jordan Creek suggests they can be important to foraging success of fish. Substrate size and current velocity are especially important to production and availability of algae, detritus, and aquatic invertebrates. Fine-particle substrates such as silt and sand, which offer unstable surfaces to invertebrates (Luedtke and Brusven, 1976), generally support fewer invertebrates than coarser, more stable substrates such as gravel and cobble (Wene and Wickliff, 1940; Resh, 1977; Waters, 1982). Substrate stability and large particle size also enhance detrital accumulation (Rabeni and Minshall, 1977) and periphyton production (Hynes, 1970). Although bluegill and longear sunfish foraged more successfully in the silt-sand area than in the gravel-cobble area, the gravel-cobble area provided more food to most species. Diet breadths were generally greater in the silt-sand area than in the gravel-cobble area, thereby suggesting that prey were less available in the silt-sand area (Pyke *et al.*, 1977). Furthermore, results from the exclosure experiments support the hypothesis that invertebrate abundance in the silt-sand area is more easily depressed by fish consumption than in the gravel-cobble area. Because resource depression is an important component of competition for food among fish (Brocksen *et al.*, 1968; Thomerson and Woolridge, 1970), this finding implies that competitive interactions are especially likely in the silt-sand area.

Low fish-food production in habitats with fine unstable substrates may be compensated by the presence of woody debris, which provides suitable colonization surfaces for many invertebrates (Nilsen and Larimore, 1973; Benke *et al.*, 1984; Angermeier and Karr, 1984). Although numerous studies document correlations between woody debris and fish abundance (Saunders and Smith, 1962; Hickman, 1975; Angermeier and Karr, 1984), influences of woody debris on foraging are largely unexamined. Nearly half of the fish groups in this study foraged more successfully in the presence of woody debris than in its absence, but three groups ate less in the presence of debris. In some cases, effects of woody debris on foraging success were most pronounced in the silt-sand area. In all cases, however, more definitive study is necessary to discern whether foraging patterns were influenced by greater availability of food, cover or both.

Virtually all Jordan Creek fishes exhibited some response in foraging success to month, year, study area or woody debris, but no factor affected all fish groups, and no two fish groups responded identically to all four factors. At some scales (*e.g.*, between-season), variation in resource availability is relatively predictable, but at others (*e.g.*, between-year) it is unpredictable, and occasionally severe (Elwood and Waters, 1969; Larimore *et al.*, 1959). Because discharge rates directly affect abundance and stability of most benthic substrates (including woody debris), the availability of foods associated with those substrates is also somewhat unpredictable. Although long-term average productivity of a stream may remain constant, variation in food availability at small spatio-temporal scales is probably continuous. Because a particular change in flow rate or substrate composition does not affect the foraging success of all species in the same direction or magnitude, frequent changes in flow and substrate conditions may preclude species from enjoying ideal foraging conditions over extensive areas or periods. Some Jordan Creek fishes (*e.g.*, centrarchids) specialize on one food resource (*e.g.*, aquatic invertebrates) even under conditions of low availability, but others (creek chub, striped shiner) opportunistically consume a variety of foods. The relative adaptiveness of either

strategy depends on the schedule of "ecological crunches" (*sensu* Wiens, 1977) for particular food resources. A collapse in the abundance of aquatic invertebrates may severely impair foraging success of centrarchids, but a similar impact on creek chub or striped shiner would require the simultaneous collapse of all food resources.

Anthropogenic modifications of watersheds and streams can dramatically alter the environmental regime under which biological communities are organized. Large-scale perturbations such as clearing, channelization and intensive cultivation alter hydrologic patterns, channel morphometry, and sediment loads (Bulkley *et al.*, 1976; Griswold *et al.*, 1978), and thus influence all levels of a stream's biological productivity (Marzolf, 1978). General accounts of midwestern fishes (Pflieger, 1975; Smith, 1979; Trautman, 1981), as well as analyses of particular river systems (Karr *et al.*, 1985), indicate that species composition and abundance of stream fishes have changed markedly since 1900. Trophic composition has typically shifted from predominance of insectivorous species to predominance of omnivores including carp and goldfish (Karr and Dudley, 1981; Karr *et al.*, 1985). This trend may reflect reduced dependability of aquatic invertebrates as a food resource, and increased frequency of ecological crunches. Comprehensive information on foraging response of fish to spatio-temporal variation in their food resources, along with knowledge of human impacts on that variation, will be useful to resource managers charged with curbing further losses of stream fishes.

APPENDIX A

Percent numerical composition of prey found in stomachs of Jordan Creek fishes. Blank cells indicate that a prey taxa contributed less than 1% of all prey items identified from a particular fish group

		Percent of total prey																		
Fish group, (age)	Total prey	Terrestrial	Annelida*	Cladocera	Copepoda	Ostracoda	Isopoda	Amphipoda	Decapoda	Hydracarina	Ephemeroptera	Odonata	Hemiptera	Megaloptera	Trichoptera	Coleoptera	Diptera	Mollusca	Fish
bluntnose minnow (0-1)	2436			42		46							2		9				
creek chub (0)	102	39	8						5		10		4	8	23				
creek chub (1)	43	23	2				2	2	9		21			28	9	9			
striped shiner (0)	400	27	2			13	1		3			2	17	2	33				
striped shiner (1)	425	47	1						6		4		9	8	23				
spotfin shiner (0-1)	173	43				1			6				14	1	31		2		
blackstripe topminnow (0-1)	345	17			5	31	3	11	2						31				
hornyhead chub (0)	831	3	3		7			4	3		2		11	11	54				
hornyhead chub (1)	684	7	1					2		8		21		13	10	25	10		
smallmouth bass (0)	634	3					6			23		57			6		2		
rock bass (0)	235	3			9		13	24	10	3	17		5		14				
rock bass (1)	89	9	1			3	6	7	12	11	33		7	3	8				
bluegill (1)	1592	4		30			3	9	5	3		9	4		32				
longear sunfish (0)	2127			27	1	5	4		5		2		2	2	52				
longear sunfish (1)	3244	2		1		4	3		9		1		3	2	72				

*Also includes Nematomorpha

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